

## Behavior of the Intertidal Gastropod *Planaxis sulcatus* (Cerithiacea: Planaxidae) in Fiji: Are Responses to Damaged Conspecifics and Predators More Pronounced on Tropical Versus Temperate Shores?<sup>1</sup>

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**ABSTRACT:** The intertidal herbivorous snail *Planaxis sulcatus* (Born) showed different avoidance behavior in response to crushed conspecifics than that to whole or crushed *Morula anaxeres* (Kiener). Addition of a crushed conspecific to pools containing *P. sulcatus* caused most individuals to move until they had reached crevices, but addition of the predatory gastropod *M. anaxeres* caused most *P. sulcatus* to move upward until they were no longer submerged. *Planaxis sulcatus* that had moved to crevices in response to crushed conspecifics climbed upward until no longer submerged after *M. anaxeres* was added to pools. It is suggested that crushed conspecifics are a cue for shell-crushing predators, which may be escaped by moving to crevices. However, such behavior provides little or no protection against a drilling gastropod compared with climbing upward until no longer submerged. The rapid and almost unanimous avoidance response of *P. sulcatus* was contrasted with the less uniform and relatively slower responses of two temperate species, *Littorina unifasciata* Philippi and *Littorina cincta* Quoy & Gaimard, to their local predators. It is suggested that differences in avoidance behavior may indicate increased predation pressure at lower latitudes.

THERE HAVE BEEN numerous reports of marine invertebrates, especially gastropods, avoiding species known to be predatory (e.g., Bullock 1953, Feder 1963, Yarnall 1964, Edwards 1969, Phillips 1975, 1976, Geller 1982, Pitcher and Butler 1987). These reports have ranged from observations of species moving rapidly away or gyrating when touched by the predator to controlled and replicated experiments with quantitative data on rates of movement, or the numbers in an area before and after addition of predators. Some invertebrates also respond to the effluent from damaged conspecifics (Snyder 1967, Hadlock 1980, Parker & Shulman 1986, McKillup and McKillup 1992), and from these studies it has been suggested that for some species, effluent from crushed conspecifics is a cue for the

presence of predators. Rittschof (1980) showed that hermit crabs are attracted by effluent from damaged conspecifics and argued that the benefit of acquiring a larger shell may outweigh the risk of predation while doing so, and also presented evidence for a decision between approach and avoidance that varies depending upon the need for a new shell (Rittschof et al. 1992).

We report on two responses by the intertidal gastropod *Planaxis sulcatus* (Born) in Fiji: crevice seeking in response to crushed conspecifics and climbing upward until no longer submerged in response to the predatory gastropod *Morula anaxeres* (Kiener).

### MATERIALS AND METHODS

Experiments were done during low tide in intertidal pools between mid tide level (MTL) and average high tide level on a rocky shore

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on Tokoriki Island, Mamanuca Group, Fiji (177° E, 17.7° S).

*Planaxis sulcatus* was mostly found in intertidal pools between MTL and extreme high water spring (EHWS). *Morula anaxeres* was only found below MTL unless in intertidal pools, where it occurred as high as average high tide level.

#### *Survey of the Shore for Distribution of Morula anaxeres and Planaxis sulcatus*

The first 25 intertidal pools above MTL encountered by two observers walking along the shore at low tide were examined for the presence or absence of *M. anaxeres* and *P. sulcatus*.

#### *Response of Planaxis sulcatus to Whole Morula anaxeres, Whole Cellana sp., and Whole Nerita polita*

Thirty pools, each with a surface area between 210 and 360 cm and that contained at least five *P. sulcatus*, were identified with wax crayon on a nearby dry surface. The following five treatments, each replicated six times, were assigned at random to the pools: addition of either one *M. anaxeres*, an unidentified herbivore (*Cellana* sp.) common on the shore at Tokoriki, *P. sulcatus*, a small stone, or no treatment. Replicates were not run simultaneously because it was not possible to find 30 pools containing *P. sulcatus* that were sufficiently close to count submerged snails quickly; instead, one replicate of each treatment was run six times, as six blocks, using 30 different pools over 2 days. For each block the numbers of submerged *P. sulcatus* were counted in all five pools, treatments were added simultaneously, and the behavior of *P. sulcatus* was observed during the following 2 min.

#### *Responses of Planaxis sulcatus to Crushed and Whole Morula anaxeres and Planaxis sulcatus*

After the observation of movement of submerged *P. sulcatus* after an accidentally

crushed conspecific fell into a pool, the above experiment was repeated using the same blocked design, but with the following treatments only: addition of either crushed or whole individuals of *M. anaxeres*, *P. sulcatus*, or the herbivore *Nerita polita* Linnaeus. The number of pools available prevented the inclusion of controls for time (the untouched pool) or disturbance (the stone), but all pools shared the common feature of one gastropod being added. Within this level of disturbance, responses to crushed and whole conspecific, predator, and herbivore could be compared. Eight replicates of treatments using *M. anaxeres* and *P. sulcatus* were run, but only five of each of the two *N. polita* treatments were run because of a shortage of pools containing *P. sulcatus*. The submersed rock lining each pool was defined as either a crevice (any crack in the rock deeper than 0.5 cm and where two surfaces intersected at less than 90°) or open rock (smooth rock without cracks) and was easily assigned to these two categories because all cracks in the rock were sufficiently deep and steep-sided to be described as crevices. The numbers of *P. sulcatus* in crevices and on open rock were counted before and 5 min after the treatment began and behavior of snails was also observed during that time.

#### *Responses of Planaxis sulcatus in Crevices to Subsequent Addition of Morula anaxeres and Cellana sp.*

The previous experiment showed that *P. sulcatus* moved to crevices in response to crushed conspecifics (see *Results*); this experiment was designed to observe the effect of *M. anaxeres* and the *Cellana* sp. on snails that had done so. One crushed conspecific was added to each of 30 pools, each of which contained more than five *P. sulcatus*. The number remaining submerged, both on rock and in crevices, was counted after 5 min. In pools where more than two *P. sulcatus* remained in crevices, one of the following five treatments was then added: whole *M. anaxeres*, *P. sulcatus*, *Cellana* sp., a small stone, or no treatment. Each treatment was replicated six

times. Counting of snails took ca. 1 min, so one replicate of each treatment was sequentially run six times, as six blocks, during the same low tide period.

## RESULTS

### *Survey of the Shore for the Distribution of Morula anaxeres and Planaxis sulcatus*

Of the 25 pools, six contained no gastropods and 13 contained *P. sulcatus*. The remaining six contained only *M. anaxeres*, but also had a ring of emersed *P. sulcatus* around their edges, suggesting that *P. sulcatus* avoids *M. anaxeres*.

### *Responses of Planaxis sulcatus to Whole Morula anaxeres, Cellana sp., Planaxis sulcatus, and Nerita polita*

Data for the responses of *P. sulcatus* show that *M. anaxeres* greatly reduced the number of *P. sulcatus* submerged in pools, but other treatments did not (Table 1). Because of the obvious effect of *M. anaxeres*, we did not consider it necessary to carry out a statistical analysis. All *P. sulcatus* began moving upward shortly after addition of *M. anaxeres* and continued moving until emersed. In contrast,

*P. sulcatus* in the other treatments showed no or little movement during the same time.

### *Responses of Planaxis sulcatus to Crushed and Whole Morula anaxeres, Nerita polita, and Planaxis sulcatus*

Results are shown in Figure 1. Addition of crushed *M. anaxeres* caused all *P. sulcatus* to climb upward out of their pools, and all but four (of 146) showed the same response to whole *M. anaxeres*. Addition of *N. polita* or whole *P. sulcatus* had no obvious effect; the numbers of submerged snails in crevices and on bare rock were almost the same before and after treatments. In contrast, addition of crushed *P. sulcatus* resulted in some conspecifics moving out of the pool, but most moved to crevices. Snails were observed to move in all directions, only stopping if they reached a crevice while still submerged. If they did not reach a crevice, snails moved until they were no longer submerged. These observations are supported by data for eight additional pools that lacked crevices (Table 2) and where addition of crushed *P. sulcatus* resulted in all conspecifics moving in all directions, even downward, and eventually leaving the pool.

TABLE 1

NUMBERS OF *Planaxis sulcatus* SUBMERGED IN POOLS BEFORE (B) AND 2 MIN AFTER (A) THE ADDITION OF EITHER WHOLE *P. sulcatus*, WHOLE *Morula anaxeres*, WHOLE *Cellana* sp., A SMALL STONE, OR IN UNTOUCHED POOLS

	TREATMENTS									
	WHOLE <i>P. sulcatus</i>		WHOLE <i>M. anaxeres</i>		WHOLE <i>Cellana</i> sp.		SMALL STONE		UNTOUCHED POOL	
	B	A	B	A	B	A	B	A	B	A
	14	14	19	0	32	32	9	9	14	14
	13	14	7	0	8	9	34	32	21	20
	6	6	15	0	13	13	16	16	5	5
	13	13	16	1	34	34	6	6	11	11
	20	20	31	0	12	12	14	14	8	8
	7	7	5	0	15	15	13	15	10	10
Totals	73	74	93	1	114	114	92	92	69	68

NOTE: Each row of the table contains data from one block.

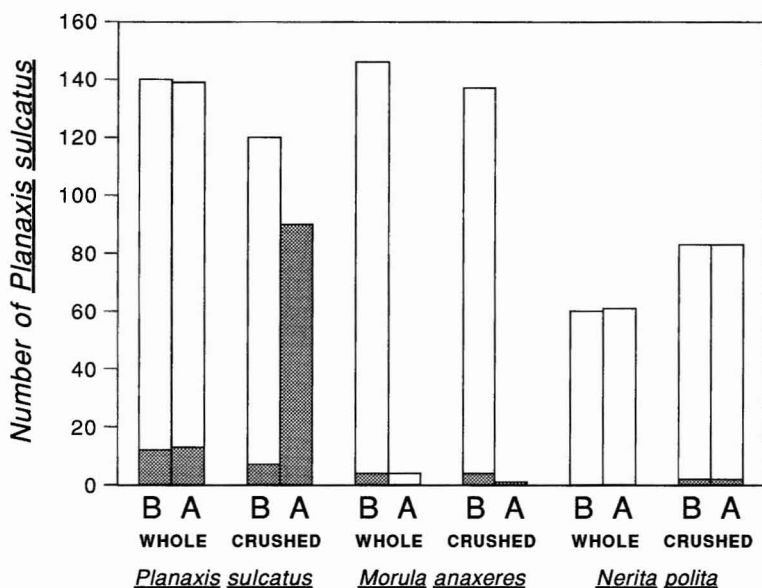


FIGURE 1. Numbers of *Planaxis sulcatus* in crevices (shaded area of bars) and on open rock within pools (white area of bars) before (B) and 2 min after (A) the addition of whole *P. sulcatus*, crushed *P. sulcatus*, whole *Morula anaxeres*, crushed *M. anaxeres*, whole *Nerita polita*, and crushed *N. polita*. Data have been summed for all replicates of each treatment.

TABLE 2

NUMBERS OF *Planaxis sulcatus* SUBMERSED IN POOLS WITHOUT CREVICES BEFORE (B) AND AFTER (A) ADDITION OF EITHER CRUSHED OR WHOLE CONSPECIFICS

WHOLE		CRUSHED	
B	A	B	A
15	15	18	0
4	4	3	0
6	6	3	0
3	3	7	0

## DISCUSSION

The experiments clearly showed that *P. sulcatus* responds to damaged conspecifics and a predatory gastropod, but not to two herbivorous gastropods common at the study site. Moving upward until no longer submerged may reduce the chance of *P. sulcatus* being drilled by *M. anaxeres* because the latter was never observed to climb out of the water. Moving to crevices in response to crushed conspecifics has been suggested to be advantageous in avoiding predation by shell-crushing crabs (Hadlock 1980). Several crab species were common on the shore at Tokoriki and 42 of 100 *P. sulcatus* examined showed signs of shell repair consistent with damage by shell-crushing predators (R.V.M., unpublished data); a snail occupying a crevice may have some protection from such a predator because it may not be as easily dislodged and crushed as one on smooth rock.

Addition of crushed conspecifics caused some *P. sulcatus* to move to crevices, but subsequent addition of *M. anaxeres* caused

#### Responses of *Planaxis sulcatus* in Crevices to Subsequent Addition of *Morula anaxeres* and *Cellana* sp.

Results are shown in Figure 2. Treatments had little or no effect upon the behavior of *P. sulcatus* occupying crevices except for the addition of *M. anaxeres*, which caused all but one of the *P. sulcatus* to leave their crevice and climb upward until no longer submerged.



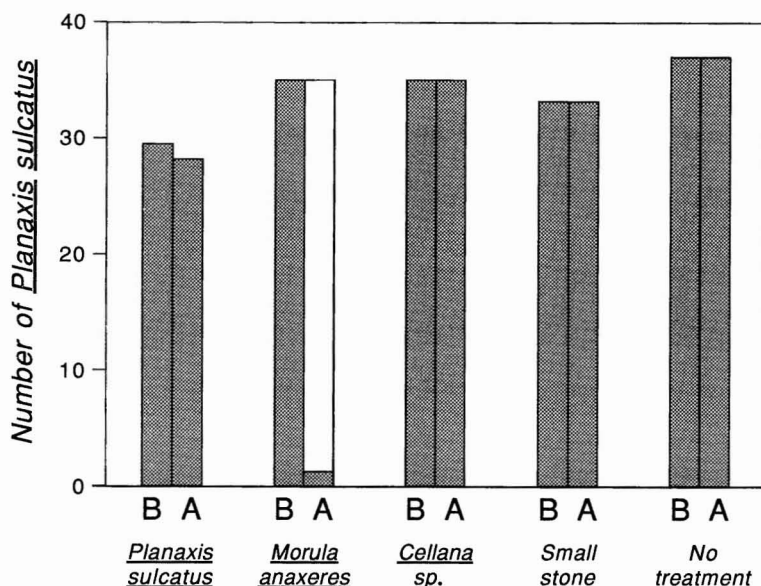


FIGURE 2. Number of *Planaxis sulcatus* in crevices before (B) (shaded area of bars) and either remaining in crevices (shaded area of bars) or climbing upward until no longer submerged (white area of bars) 2 min after (A) the addition of whole *P. sulcatus*, whole *Morula anaxeres*, whole *Cellana* sp., small stone (control for disturbance), and no treatment. Data have been summed for all replicates of each treatment.

these individuals to leave their crevices and move upward until no longer submerged. This is consistent with either (1) the response to *M. anaxeres* overriding the response to crushed conspecifics, or (2) *P. sulcatus* simply showing sequential responses to different stimuli presented at different times. The design of the experiments reported here did not enable discrimination between these two explanations, but simultaneous presentation of *M. anaxeres* and crushed *P. sulcatus* was also made in four pools with crevices (unpublished data). Although that experiment was not controlled in that there was only one treatment, all *P. sulcatus* climbed upward until they were no longer submerged, which is consistent with (1) above.

Assuming that the response to *M. anaxeres* does override that to crushed conspecifics, there are at least three possible explanations for the behavior. First, the response to an actual stimulus (presence of a *M. anaxeres*) may always override that of a token stimulus (damaged conspecifics), which may not al-

ways be associated with the presence of a predator. Second, the risk of remaining submerged with *M. anaxeres* may be greater than the risk of leaving a crevice and being attacked by a shell-crushing predator. Third, the response of *P. sulcatus* may simply be a result of the stimulus from one *M. anaxeres* being greater than the stimulus from a single crushed conspecific. It was not possible to investigate these possibilities because of the short time spent at Tokoriki.

There are obvious pitfalls in comparing results from different experimental designs, researchers, sites, and times. Nevertheless, the responses of *P. sulcatus* in Fiji were striking in that only one of 94 individuals remained submerged 2 min after the addition of *M. anaxeres* (Table 1). These results contrast with the slower and less unanimous responses shown by two other herbivorous gastropods in almost identical field experiments done by S.C.M. at two temperate sites. Thirty percent of *Littorina unifasciata* Philippi and 20% of *Littorina cincta* Quoy & Gaimard remained

submersed after 1 hr of exposure to the predatory whelk *Lepsiella scobina albomarginata* (Deshayes) at Portobello, New Zealand (McKillup 1981), whereas 58% and 39%, respectively, of *L. unifasciata* remained submersed after 1 hr of exposure to the predatory *Lepsiella flindersi* (Adams & Angas) and *Lepsiella vinosa* (Lamarck) at Coobowie, South Australia (McKillup 1982). Experiments at Coobowie and in Fiji were carried out in early summer (December) and seawater temperatures in pools were between 27 and 31°C at both sites (S.C.M., unpublished data). It has been argued that predation pressure upon intertidal gastropods increases as latitude decreases (e.g., Vermeij 1978), and this hypothesis has been supported by field experiments, including those of Bertness et al. (1981) and Menge and Lubchenco (1981). Therefore, the more rapid and almost unanimous behavioral response observed in Fiji compared with that in southern Australia and New Zealand may also reflect the greater selective pressure imposed by predators in the tropics. Nevertheless, the observed differences in behavior are not direct evidence for differences in predation pressure, and we have only compared one species from a tropical shore with two from temperate shores. Garrity and Levings (1981) reported that 67% of the tropical *Nerita scabricosta* Lamarck climbed out of a pool to which one individual of the predatory *Purpura pansa* Gould had been added, and 100% climbed out in response to addition of *P. pansa* that had been stimulated to exude fluid, and also to the fluid itself, but these experiments were unreplicated. A more extensive comparative examination of the behavior of additional species in relation to latitude may show a greater frequency and intensity of avoidance responses as latitude decreases.

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